

Reproductive biology and mating conflict in the simultaneously hermaphroditic land snail *Arianta arbustorum**

Bruno Baur

Department of Environmental Sciences, Section of Conservation Biology, University of Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland, Bruno.Baur@unibas.ch

Abstract: This review summarizes the present knowledge on the reproductive biology, mating system, sperm competition, sex allocation, and mating conflict in the simultaneously hermaphroditic land snail *Arianta arbustorum* (Linnaeus, 1758) (Helicidae). Field studies and controlled laboratory experiments indicate that mating is random with respect to shell size. However, subtle effects of inbreeding (reduced hatching success of eggs and viability of juveniles) and outbreeding were found. Individuals of *A. arbustorum* mate repeatedly with different partners and store viable sperm for more than one year. Spermatophore transfer is highly reciprocal, but the number of sperm they contain (800,000-4,000,000) is not necessarily equal. Snails need 3-4 weeks to replenish their autosperm reserves after a successful copulation. Sperm are monomorphic. However, there is considerable among-population—and to a minor extent—within-population variation in total sperm length. Sperm utilization patterns in double-mated individuals of *A. arbustorum* revealed striking differences among individuals. There is a huge variation in the structure of the spermatheca, which consists of 2-9 blind tubules. Different lines of evidence suggest that the snails might be able to store and expel sperm stored in single tubules and thus promote a selective fertilization of eggs (cryptic female choice). Maternal investment in eggs is considerable. Snails mated 1, 2, or 3 times showed that irrespective of the number of matings the individuals devoted >95% of the resources into the female function.

Key words: Gastropoda, mating system, reproductive behavior, sex allocation, sperm competition

Traditional models of sexual selection explain the evolution of secondary sexual traits (mainly in males) and preferences for reproductive partners displaying such traits (mainly in females; Andersson 1994). Although these models differ in how sexual selection operates, they all propose that partner choice increases both average male and average female fitness in a population (Pizzari and Snook 2003). Recent theoretical and empirical work, however, has stressed that sexual conflict may be a potential broker of sexual selection. When the fitness interests of females and males diverge, a reproductive strategy that increases the fitness of one sex may decrease the fitness of the other sex. In this way unequal reproductive investments per gamete (egg versus sperm) lead to sexual conflicts (Trivers 1972). In recent years, experimental evidence for sexual conflicts has been reported in a variety of gonochoristic animals (Chapman *et al.* 2003, Arnqvist and Rowe 2005). Mechanisms of sexual conflicts are of particular interest in simultaneous hermaphrodites (Michiels 1998).

In hermaphrodites, selection for female traits cannot be independent from selection for male traits of the same individual. Sexual selection for traits related to mate attraction is assumed to be weaker in hermaphrodites (Greeff and Michiels 1999a), but because many simultaneous hermaph-

rodites mate repeatedly and store sperm for long periods, they are affected by forces similar to those leading to complicated mating strategies and sperm competition in animals with separate sexes (Charnov 1996, Michiels 1998, Angeloni *et al.* 2003). However, unlike gonochoristic species, simultaneous hermaphrodites have an additional reproductive strategy; they can adjust the ratio of resources invested into reproduction in the female role versus the male role, depending on current selection pressures and environmental conditions (Charnov 1982). Sex allocation complicates sexually selected strategies because any increased investment in one sexual role results in a decreased investment in the other.

Pulmonate gastropods are excellent study organisms for determining the mechanisms and effects of sperm competition and sex-specific reproductive allocation on both the fitness of snails and the conflict between male and female function within an individual (Baur and Baur 2000). Although the theoretical framework for sexual conflicts in simultaneous hermaphrodites already exists, such conflicts have rarely been examined experimentally in terrestrial gastropods (for an exception see Chase 2007).

The aim of this review is to summarize the present knowledge on the reproductive biology, mating system,

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sperm competition, sex allocation, and mating conflict in the pulmonate land snail *Arianta arbustorum* (Linnaeus, 1758). The strength of this model system comes from the possibility of conducting field experiments and of studying the behavior of individual snails under controlled conditions; the ability to produce laboratory crosses with relative ease; and the availability of well-established techniques (e.g., to estimate the number of sperm delivered and the number of eggs produced [Locher and Baur 1997], and to measure sperm length, sperm velocity, motility and longevity [Minoretti and Baur 2006]; two novel non-invasive techniques for isolating DNA and a set of microsatellite markers which can be used for paternity analysis [Locher and Baur 2001, Armbruster *et al.* 2005]). By compiling the existing information, this review should stimulate future studies on mating systems and reproductive behavior in simultaneously hermaphroditic gastropods.

NATURAL HISTORY

Members of the species *Arianta arbustorum* are simultaneously hermaphroditic, helicid land snails common in moist habitats of northwestern and central Europe, living at elevations of up to 2700 m above sea level in the Alps (Kerney and Cameron 1979). Adult shell size diminishes with increasing elevation (population means of shell breadth ranging from 13 to 23 mm; Burla and Stahel 1983, Baur 1984a, Baur and Raboud 1988). The species shows a high phenotypic variability in shell and soft body color that is related to habitat and elevation (Burla and Stahel 1983, Gittenberger 1991, Gosteli 2005). Variation in shell color is continuous between large brown morphs, occurring mainly in forests in the lowlands, and small yellow morphs in alpine grasslands at high elevation. Population density is highly variable in *A. arbustorum*, ranging from 0.01 to 11 adults per m² (Baur 1986a, 1988a). On mountain slopes, *A. arbustorum* can be continuously distributed over large areas and thereby reach huge population sizes (Baur 1986a). In contrast, partly or completely isolated populations consisting of only a few individuals can persist in small patches of marginal habitat (Baur 1993a, Akçakaya and Baur 1996). Information on patterns of daily movement and dispersal in *A. arbustorum* can be found in Baur (1986a), A. Baur and B. Baur (1990, 1992, 1993), Baur *et al.* (1997), and Kleewein (1999).

Arianta arbustorum has determinate growth. Sexual maturity is attained after the completion of shell growth. However, matings involving individuals that had not yet finished their shell growth have been observed in a few cases (Baur 1984b). Age at maturity increases from 2 years in snails living in the lowlands to 5 years in individuals in alpine populations, but median adult longevity (3-3.5 years; maximum 14 years) and adult survival rates (0.5-0.7 per year) are

approximately the same at all elevations (Baur and Raboud 1988). Individuals of *A. arbustorum* mate repeatedly during the reproductive season (Baur 1988b). In the field, snails deposit one to three egg batches, each consisting of 20-60 eggs, per reproductive season (Baur and Raboud 1988, Baur 1990a, B. Baur and A. Baur 1993). During the winter snails hibernate in leaf litter or soil (Terhivuo 1978).

Arianta arbustorum exhibits large interpopulational genetic variation (Arter 1990, Haase *et al.* 2003) and shows considerable variation in behavior and rate of parasitic infestation (Baur 1986b, 1994a, Baur and Gosteli 1986, Baur and Baur 2005). In some populations, individuals of *A. arbustorum* are infested by the mite *Riccardoella limacum* which sucks blood and lives in the snails' lungs. Prevalence of mite infection ranged from 45.8 to 77.8% in four natural populations of *A. arbustorum* while in seven other populations no infected snails were found (Baur and Baur 2005). Information on density-dependent growth and potential predators on *A. arbustorum* is summarized in Reichardt *et al.* (1985). Aspects of food choice in *A. arbustorum* have been examined by Speiser and Rowell-Rahier (1991, 1993) and Speiser *et al.* (1992).

MODE OF REPRODUCTION

Arianta arbustorum was long believed to reproduce exclusively by cross-fertilization (Lang 1904). Chen (1994) reared 44 individuals in isolation from the subadult stage and recorded their reproductive performance for 1, 2, or 3 years under laboratory conditions after they had attained sexual maturity. The snails produced eggs without being mated, however, in a significantly lower number than did mated control snails. In their first reproductive season, only 1 egg hatched out of 284 eggs (hatching success 0.4%) produced by 33 snails. In the second reproductive season, 32 of the 671 eggs laid by 29 snails hatched (hatching success 4.8%). In the third reproductive season, 23 of the 191 eggs laid by 6 snails hatched (hatching success 12.0%). The percentages of snails that laid fertile eggs were 3.0% (1 of 33 snails), 31.0% (9 of 29 snails), and 33.3% (2 of 6 snails), respectively, for the 3 years after maturation. The number of hatchlings produced by unmated snails was 1-2% of that produced by mated snails of the same age. This indicates that *A. arbustorum* is able to self-fertilize, but with a great reduction in fitness. Cross-fertilization is the dominant mode of reproduction in this species. Self-fertilization might occur only if no mating partners were available over long periods.

MATING PATTERNS

Size-assortative mating is a common pattern in natural populations of many invertebrate and vertebrate species.

Hermaphroditic land snails would greatly enhance their reproductive success by choosing large mates since female fecundity (number of clutches, clutch size, and egg size) is positively correlated with shell size (Wolda 1963, Baur 1988a, Baur and Raboud 1988). Ridley (1983) suggested that size-assortative mating patterns should occur in simultaneously hermaphroditic land snails with reciprocal fertilization and size-related female fecundity. He argued that all individuals invest substantially (all their eggs) in mating, so there will be selection for careful mate choice. In another approach, Parker (1983) proposed a model for indiscriminate mate choice (random mating). This should occur when there is little variance in mate quality in both sexes, and/or when search costs for mates are high (e.g., low encounter rates due to low population densities or low mobility). Baur (1992a) examined mating patterns in natural populations of *Helix pomatia* Linnaeus, 1758 and *Arianta arbustorum*. In a large population of *H. pomatia* (700-1000 individuals) in Sweden, snails showed a slight (but non-significant) tendency towards size-assortative mating, whereas mating in a subalpine population of *A. arbustorum* in Switzerland was random with respect to size. Baur (1992a) also conducted controlled choice experiments to test whether individuals of *A. arbustorum* discriminate between mating partners of different sizes and whether a large shell size might be of advantage in groups of courting snails to increase mating success. In mate-choice tests with snails of different shell size, pairs formed randomly with respect to size. Courtship was neither hindered nor prolonged in pairs with large size differences. In the second experiment, a large *A. arbustorum* was placed close to two courting conspecifics (both smaller). The larger snail interfered with the courting snails, but in general did not displace one of them. Courtship progressed to copulation only if one of the three snails ceased to court; this was independent of the size of the individual. Thus, a large shell did not increase mating success. Time-constraints of locomotory activity and high costs of searching for a mate can explain the prevalence of random mating patterns in simultaneously hermaphroditic land snails (Baur 1992a).

Mating has also been reported to be random with respect to shell size, shell color, and banding pattern in *Cepaea nemoralis* (Linnaeus, 1758) (Schilder 1950, Schnetter 1950, Lamotte 1951, Wolda 1963). Mating was also random between resident and introduced individuals of *Helix pomatia* (Woyciechowski and Lomnicki 1977). Mate-choice tests with *Arianta arbustorum* from geographically isolated populations in Sweden and Switzerland revealed that snails from three populations preferred to mate with snails from their population of origin although no interpopulational differences in latency or duration of courtship were found (Baur and Baur 1992a). Mating preferences could partly be explained by differences in mating propensity in two of the

three populations, but not in matings between a Swedish and a Swiss population. Cross-breeding demonstrated a high degree of reproductive compatibility between these two distant populations. In contrast, pairs involving individuals from two distant Swiss populations had a reduced fertility. The experimental results indicate effects of outbreeding depression between distant populations of *A. arbustorum*. However, the extent of outbreeding depression seems not to be related to the geographical distance between populations.

Mating between closely related individuals can incur substantial fitness costs (i.e., inbreeding depression). For simultaneous hermaphrodites such as *Arianta arbustorum*, inbreeding depression is regarded as the most important selective force acting against self-fertilization, and maintaining outcrossing (Ghiselin 1969, Jarne and Charlesworth 1993). B. Baur and A. Baur (1997) performed mate-choice tests to examine whether individuals of *A. arbustorum* discriminate between full-sibs and non-sibs from the same population and whether incestuous matings reduce the snails' subsequent reproductive success. Full-siblings (F_1) were raised under laboratory conditions. Snails mated randomly with respect to the degree of relatedness, indicating a lack of inbreeding avoidance by selective mating. Snails that mated with full-sibs did not differ in number of eggs, hatching success of eggs, or number of offspring produced from those mated with unrelated conspecifics. In another breeding experiment with *A. arbustorum* from a different population, Chen (1993) compared the reproductive performance of snails that mated with full-sibs to that of snails that mated with unrelated partners. Again, there was no difference in the number of eggs produced. However, eggs of inbred snails showed a lower hatching success (30.4%) than those of outbred snails (48.5%). Thus, inbred snails had fewer hatchlings. Furthermore, inbred offspring reared in the garden had a higher mortality rate than outbred offspring reared in the same environment, but no difference was found when offspring from both groups were kept in the laboratory. This result supports the hypothesis that cross-fertilization in simultaneous hermaphrodites is maintained by inbreeding depression. It also shows that the extent of negative inbreeding effects vary among populations and environments in which the snails are kept.

MULTIPLE PATERNITY IN THE WILD

The genetic background of shell polymorphism, including ground color and banding pattern, is well studied in *Arianta arbustorum* (Oldham 1934, Cook and King 1966). One locus controls the ground color of the shell, which may be yellow or brown (brown being dominant). Thus, shell color can be used as a genetic marker to analyze paternity in



Figure 1. Copulating pair of *Arianta arbustorum* in an alpine grassland in Switzerland (photo: B. Baur).

broods of double-mated individuals of known genotype because shell color is already distinctly expressed in hatchlings. Twenty-two adult *A. arbustorum* with yellow shells were collected in a pasture on Mt. Raimeux (Jura mountains, Switzerland) at an elevation of 1290 m (B. Baur 1994b). This population is dimorphic with respect to shell color. Two estimates revealed very similar results: 27.7% ($n = 94$) of the adult *A. arbustorum* had yellow shells on 20 May 1993 and 27.4% ($n = 124$) on 24 July 1993. Assuming Hardy-Weinberg equilibrium, the frequency of the allele "brown" is estimated to $p = 0.475$ and that of the allele "yellow" to $q = 0.525$. Of the 22 adult *A. arbustorum*, 19 produced 34 clutches with fertilized eggs in the laboratory. Nine of the 34 clutches (26.5%) deviated significantly from Mendelian ratios of single paternity, providing evidence for multiple paternity (B. Baur 1994b). This figure may underestimate the actual frequency of multiple paternity because repeated matings with snails of the same genotype will produce results that are indistinguishable from the broods of single matings. Several snails deposited 2 or 3 clutches. Considering the total number of offspring produced by single snails during 65 days, the progeny of 12 of 19 individuals (63.2%) deviated significantly from Mendelian ratios of a single copulation.

SPERM COMPETITION

Sperm competition, the competition between spermatozoa from different males to fertilize the eggs of a single female during one reproductive cycle, is a form of male-male competition that occurs between insemination and fertiliza-

tion (Parker 1970). It is a part of intrasexual selection. Sperm competition has been solely treated as a male-male conflict over many years, with females being an inert arena in which the conflict occurs. More recently, female processes that affect male reproductive success and that occur after copulation have received increasing attention: cryptic female choice and selective sperm use (Eberhard 1996, see below).

Courtship and dart shooting

During courtship, many helicid snails attempt to pierce the body walls of their mating partners with mucus-coated calcareous darts (Koene and Schulenburg 2005). The mucus covering the dart induces conformational changes in the female reproductive tract of the recipient, closing off the entrance to the gametolytic bursa copulatrix. In *Helix aspersa* O. F. Müller, 1774, a pulmonate land snail with obligate dart shooting, individuals that were hit by darts stored significantly more sperm than did snails that were missed (Landolfi *et al.* 2001, Rogers and Chase 2001, 2002, Landolfi 2002, see also Chase 2007).

In *Arianta arbustorum*, dart shooting is not an obligatory element of courtship behavior. Baminger *et al.* (2000) examined dart shooting in relation to different aspects of sperm competition (allosperm storage and autosperm delivery) in three natural populations of *A. arbustorum* in the Eastern Alps, Austria. Twenty-six (30.2%) of the 86 copulating snails used their darts. There was no reciprocity in dart shooting: individuals shot their darts independently of the behavior of their mating partners. Further, the occurrence of dart shooting was related neither to the number of sperm delivered nor to the number of sperm received from the partner. Finally, the occurrence of dart shooting was not influenced by the amount of allosperm stored from previous matings. In laboratory matings of *A. arbustorum* from Mt. Raimeux, Swiss Jura mountains, 50% of the copulating individuals pushed or tried to push a dart into their partners (Bojat and Haase 2002). Dart recipients did not store more sperm than snails not hit by the dart. This indicates that the importance of dart shooting for sperm storage varies among species of snails and even among populations of the same species.

Spermatophore formation and sperm transfer

In *Arianta arbustorum*, the spermatophore has a distinctive form consisting of head filament, sperm container, and a 2-3 cm long tail. The spermatophore is formed in the epiphallus (head filament and sperm container) and in the flagellum (tail) during copulation (Hofmann 1923). Baminger and Haase (2001) examined formation and filling of spermatophores by collecting spermatophores in mating

pairs of *A. arbustorum* at certain intervals after the beginning of copulation. Two minutes after penis intromission there was no trace of a spermatophore. After 5 min, a spermatophore without tail was visible in two of four individuals. After 10 min, each snail contained a complete, albeit small, spermatophore consisting of head filament, container, and fully-developed tail. The part of the spermatophore that contained the sperm was increasing in size until shortly before the spermatophore was transferred (approx. 90 min after penis intromission). Spermatophore formation was initiated more or less synchronously in mating partners shortly after the beginning of copulation. However, the growth and final size of the spermatophore were not adjusted between the mating partners. These observations are supported by the finding that the numbers of sperm transferred by two mating snails are not correlated (Baur *et al.* 1998). This also indicates that sperm trading (sensu Leonard 1991) does not occur in *A. arbustorum* (see also number of sperm delivered).

The form of the spermatophore in *Arianta arbustorum* is very similar to that in *Helix pomatia* (Lind 1973), except that the head of the spermatophore is proportionally shorter and not filamentous in the latter species (Hofmann 1923). The tail, with its spiral cross section, especially suggests that the function is identical in both species (Baminger and Haase 2001). After spermatophore transfer, only sperm that migrate through the tail, which reaches deep into the vagina, can bypass the digesting bursa copulatrix and reach the spermatheca through which they travel to the spermatheca, where they are stored. The head filament probably guarantees that the spermatophore is not pushed too far up into the diverticulum, preventing the tail from getting too close to the entrance of the bursal duct. The dissolution of the spermatophore in the female tract of the receiver takes more than one week in *A. arbustorum* (Haase and Baur 1995).

Number of sperm delivered

Sperm number, in some cases, is an important determinant for achieving successful fertilization in sperm competition (Birkhead and Møller 1998). Theoretical models and empirical evidence from various studies suggest that, fundamentally, numerical superiority is an adaptive strategy for sperm competition (Parker 1990a, 1990b, Birkhead and Møller 1998). However, males may incur a substantial cost in the production of ejaculates and spermatophores (Dewsbury 1982, Nakatsuru and Kramer 1982). Parker's model (1990a, 1990b) predicts that males faced with an increased risk of sperm competition should maximize the prospects of fertilization by inseminating more sperm per ejaculate. For example, owing to sperm storage from previous copulations, mating with a nonvirgin partner may result in a higher risk of sperm competition than mating with a virgin partner.

Experimental evidence for adjustment of ejaculate size with respect to mating history has been provided for insects, salamanders, rats, and humans (Birkhead and Møller 1998). In other species, however, males do not adjust the size of their ejaculates to the mating history (e.g., in zebra finches, Birkhead and Møller 1998).

An adjustment of the number of sperm released is also a prerequisite for sperm trading. In simultaneous hermaphrodites, a sexual conflict may arise when there is a difference in potential fitness gain between the role of the sperm donor and that of the sperm receiver (Charnov 1979, Leonard 1991). Hermaphroditic individuals in a population would benefit from mating primarily in the more fitness-enhancing sexual role, leading to a conflict of interest between two prospective mating partners (Charnov 1979). Gamete trading might have evolved to resolve the sexual conflict in simultaneous hermaphrodites (Leonard 1991). The gamete-trading model is based on the premise that the preferred role for a simultaneous hermaphrodite will be the one that controls fertilization (Leonard 1991). In particular, this model predicts that where the female function controls fertilization, the mating system will be based on sperm trading.

Baur *et al.* (1998) examined whether individuals of *Arianta arbustorum* adjust sperm release according to the potential risk of sperm competition incurred with a virgin or nonvirgin mating partner and whether sperm trading occurs in mating pairs. In controlled mating trials, focal snails were allowed to copulate with virgin or nonvirgin partners to simulate a different risk of sperm competition in a given mating. The number of sperm transferred ranged from 802,620 to 3,968,800 (mean = 2,185,100; $n = 91$), but was related neither to the mating history of the partner nor to the duration of the copulation. This indicates that individuals of *A. arbustorum* are not able to adjust sperm expenditure to the mating history of the partner. Furthermore, the number of sperm transferred was correlated neither with the size of the donor nor with the size of the recipient. There was, however, a high degree of reciprocity in spermatophore transfer: in 45 of the 46 mating pairs investigated both partners delivered a spermatophore that contained spermatozoa. In contrast, the numbers of sperm transferred by the two mating partners were not correlated. This indicates that sperm trading does not occur in *A. arbustorum*.

Locher and Baur (2000a) examined the effect of increased risk of sperm competition on male and female reproductive traits in individuals of *Arianta arbustorum*. In a laboratory experiment snails were exposed to mucous trails of conspecifics, simulating a high risk of sperm competition. Courtship behavior, spermatophore size, and number of sperm delivered were not influenced by a higher risk of sperm competition. However, snails constantly exposed to mucous trails of conspecifics deposited more egg batches

than snails denied any cues from conspecific mucous trails. This indicates that *A. arbustorum* does not respond to experimentally increased cues from conspecifics, which were assumed to mimic a high risk of sperm competition by delivering more sperm.

Number of matings and intermating interval

Multiple mating is common in helcid snails. Individuals of *Helix pomatia*, *Cepaea uenoralis*, and *Arianta arbustorum* have been observed to mate repeatedly with different partners in the course of a reproductive season, resulting in multiple-sired broods (Wolda 1963, Murray 1964, B. Baur 1988b, 1994b). Individuals of *Helix pomatia* copulated 2-6 times per year in a Danish population (Lind 1988) and 2-4 times in a German population (Tischler 1973). Individuals of *H. aspersa* copulated on average 3 times (maximum 7 times) in a British population (Fearnley 1993, 1996). Actual records on the number of matings in natural *A. arbustorum* populations are not available. Video-recording of *A. arbustorum* kept in groups of six snails under laboratory conditions revealed that individuals copulated between 0 and 3 times in a period of 58 days (N. Minoretti, pers. comm.). Furthermore, paternity analysis in egg batches of *A. arbustorum* sampled in a natural population indicated that at least 63% of the snails used sperm from two or more mates to fertilize their eggs (B. Baur 1994b).

The few data available on mating frequency in gastropods suggest that terrestrial gastropods copulate less frequently than freshwater and marine gastropods (Baur 1998). In intertidal and terrestrial gastropods the reproductive activity is limited by favorable environmental conditions. The long-lasting courtship and mating behavior of terrestrial gastropods may exceed the period favorable for locomotory activity (the high risk of desiccation may incur a significant cost of mating). Freshwater and marine habitats, however, may provide temporally more constant conditions favorable for mating activities than terrestrial habitats. Other explanations for the relatively small number of copulations in terrestrial pulmonates include the costs of producing mucus during mating, the production of spermatophores and darts (in some species), and the large number of sperm delivered during a copulation, which may result in sperm depletion.

Locher and Baur (1999) showed that individuals of *Arianta arbustorum* needed at least 8 days to replenish their sperm reserves after a successful copulation. Furthermore, the number of sperm delivered in the second copulation increased with an increasing intermating interval from 6 to 29 days. This finding suggests that the number of sperm delivered increases with even longer intermating intervals. Hänggi *et al.* (2002) examined the size of the spermatophore and the number of sperm delivered in two groups of *A.*

arbustorum that remated either after 3-4 weeks or after 7-8 weeks. The results indicated that *A. arbustorum* entirely replenishes its autosperm reserves within 3-4 weeks after a successful copulation.

Sperm size and quality

Much interest has also been focused on theory concerning the significance of the size and quality of sperm (*e.g.*, Parker 1982, Parker and Begon 1993, Pizzari and Birkhead 2002). The size of sperm may influence their power and swimming speed as well as longevity because of changes in the energetic demands of longer or shorter flagella. For example, in echinoids that use broadcast spawning, there is evidence that sperm velocity and longevity covary between and within species (Levitan 1993). Levitan (2000) has shown that in a sea urchin, sperm velocity and longevity are traded off against each other. In taxa with sperm storage organs, sperm length may determine the ability to reach the storage organs first and to move to the ovum from the storage organs once ovulation takes place. However, assuming a fixed resource budget, smaller sperm may allow males to produce more gametes, which may be adaptive if sperm compete numerically (Parker 1982). Confounding variables, such as the morphology and biochemistry of the female reproductive tract, might also affect sperm form and function.

Besides the size and number of sperm transferred, the quality of ejaculates (proportion of live, morphologically normal spermatozoa and motility of spermatozoa) might be important in determining the outcome of sperm competition. Indeed, recent studies in gonochoristic animals reveal substantial intraspecific variation in sperm motility and longevity. This variation may function in postcopulatory sexual selection. A synthesis of the available literature indicates that these sperm-quality traits affect fertilization success and that they are important in both sperm competition and cryptic female choice (Snook 2005).

Molluscan sperm are characterized by a remarkable array of morphological features (Thompson 1973, Anderson and Personne 1976, Hodgson *et al.* 1996). The interspecific variation in sperm morphology is frequently used as a taxonomic character. Data on sperm length are available for several gastropod species. Spermatozoa of terrestrial pulmonates are among the longest of the molluscs (*e.g.*, 850 μm in *Helix pomatia*; Thompson 1973). However, intraspecific variation in sperm length and quality has not been analyzed in any hermaphroditic gastropod species.

Minoretti and Baur (2006) developed techniques to measure sperm length, sperm velocity, percentage motility, and longevity of sperm in *Arianta arbustorum*. They examined variation in sperm length in individuals from four natural populations and variation in velocity, motility, and

longevity of sperm in two populations. Sperm of *A. arbustorum* are monomorphic. Like other pulmonates, *A. arbustorum* produces extremely long sperm. Independent of shell size, sperm length differed among populations (mean values of populations: 878, 898, 913, and 939 μm) and—to a minor extent—even among individuals within populations. Mean sperm length of a snail was not correlated with the number of sperm delivered in a spermatophore. Individual snails showed consistent sperm length in successive matings. The mean sperm velocity was not influenced by shell size, nor did it differ between populations. However, mean sperm velocity differed among individual snails (range 52–112 $\mu\text{m/s}$). Percentage motility and longevity of sperm differed between snails from different populations but were not affected by shell size. No correlations were found between length, velocity, percentage motility, and longevity of sperm. Thus, individual snails differed in sperm quality. This interindividual variation may partly explain differences in fertilization success.

Sperm precedence

Sperm precedence is the differential sperm usage from consecutive matings (mating order effect). It is typically measured as the proportion of eggs fertilized by the second of two mates (the P_2 value). Patterns of sperm utilization were investigated in double-mated individuals of *Arianta arbustorum* (B. Baur 1994b). In particular, the effects of delay between copulations (range 9–380 days) and size of the sperm donor on sperm precedence (P_2) were examined. Using shell color as a genetic marker, paternity was analyzed in 132 broods produced by 35 snails that had mated with two partners of different genotypes. Sperm precedence (P_2) was influenced by the time between the two matings when the mating delay exceeded 70 days (one reproductive season). In the first brood of snails that mated twice within 70 days, P_2 averaged 0.34, indicating precedence of sperm from the first mate. In contrast, P_2 averaged 0.76 in broods of snails that remated in the following season, indicating a decreased viability of sperm from the first mate. The size of sperm-donating individuals had no effect on the fertilization success of their sperm in the first brood produced after the second copulation. Analysis of long-term sperm utilization in 23 snails that laid 3–9 batches over 2 years revealed striking differences among individuals. Five snails (21.7%) exhibited precedence of sperm from the first mate throughout, 8 snails (34.8%) showed precedence of sperm from the second mate throughout, whereas 10 snails (43.5%) exhibited sperm mixing in successive batches. This indicates that different mechanisms might be involved in creating the observed inter-individual variation in sperm precedence.

FEMALE ROLE IN SPERM COMPETITION: CRYPTIC FEMALE CHOICE

Until recently, most research concentrated on male aspects of sperm competition in gonochoristic animals. In the past few years, there has been increasing interest in the possibility that females influence the outcome of sperm competition by cryptic female choice and selective sperm use (Eberhard 1996). Females might be able to discriminate between and differentially utilize the sperm of different males, a process referred to as 'sperm choice' (Birkhead 1998). There are broad and narrow definitions of "sperm choice"; some authors make it synonymous with "cryptic female choice" (see Eberhard 2000, Kempnaers *et al.* 2000, Pitnick and Brown 2000). Cryptic female choice has been defined as nonrandom paternity biases resulting from female morphology, physiology or behavior that occur after coupling (Pitnick and Brown 2000). This definition ascribes to sperm choice any biases in paternity owing to the way females handle sperm, regardless of the specific mechanism or evolutionary causes, and regardless of proximate control. The only relevant consideration for this definition is whether a female-mediated process generates sexual selection on males. A general problem with cryptic female choice is that it is difficult to rule out the direct influence from males (*e.g.*, Edvardsson and Arnqvist 2000).

In simultaneously hermaphroditic pulmonates the role of the female duct is to receive sperm from a copulating partner, to store the sperm, to provide a site for fertilization, to form the egg capsule, and to digest sperm and remnants of the spermatophore so as to absorb nutritional fluids received with the ejaculate.

Variation in the morphology of the female reproductive tract

Rapid evolution of reproductive traits has been attributed to sexual selection arising from interactions between the sexes (*e.g.*, Eberhard 1996). Inter- and intraspecific studies in gonochoristic animals revealed a covariation between sperm characteristics and the size of the female reproductive tract, indicating an evolutionary divergence, which is consistent with the theory of post-copulatory sexual selection. In *Arianta arbustorum*, like other terrestrial pulmonates, the enormous variation in structure and morphology of the spermatheca, fertilization chamber, and sperm digesting organ could have evolved in response to different levels of sperm competition and/or cryptic female choice (Baur 1998). Baminger and Haase (2000) examined the variability of the distal genitalia involved in spermatophore production, reception, and manipulation in 113 adult individuals of *A. arbustorum* from six natural populations. In particular, Baminger and Haase (2000) asked whether the variation in

genitalia is related to the intensity of sexual selection, measured as local population density. The size of the genitalia was unexpectedly inversely related to population density, probably because of an increased inhibitory effect of snail mucus. Patterns of variation of female and male characters did not differ. However, the influence of sexual selection on genitalia size and variance could not be unambiguously determined.

Beese *et al.* (2006a) quantified the variation in male and female reproductive traits among six natural populations of *Arianta arbustorum* and examined the covariation in interacting traits. There was a significant among-population variation in spermatophore volume, number of sperm transferred, and sperm length, as well as in volume of the sperm storage organ (spermatheca) and number of tubules, but not in spermathecal length. Furthermore, there was no relationship between sperm size and spermathecal length. There was, however, a positive association between the number of sperm transferred and spermathecal volume. This result suggests that the same post-copulatory mechanisms that operate in gonochorists drive the correlated evolution of reproductive characters in hermaphrodites.

The wall of the spermatophore received is dissolved in the bursa tract diverticulum (Beese *et al.* 2006b). The digested material is taken up by epithelial cells.

Organ for sperm storage

Individuals of *Arianta arbustorum* are able to store viable sperm from different mating partners for more than 1 year (Baur 1988b). The morphology of the sperm storage organ (spermatheca) may influence the outcome of sperm competition in *A. arbustorum*, as shown in insects (Simmons and Siva-Jothy 1998). *Arianta arbustorum* shows a considerable variation in the structure of the spermatheca (Haase and Baur 1995, Beese and Baur 2006). It consists of two to nine blind tubules uniting to a common duct, which opens into the fertilization chamber (Haase and Baur 1995, Baminger and Haase 1999, Baminger *et al.* 2000). The musculature surrounding the spermathecal tubules is arranged in a complex three dimensional network (Bojat *et al.* 2001a, 2001b, 2001c). If there were a selective activation of the muscles of each tubule (which has not yet been examined), this would allow the animal to expel sperm stored in single tubules and thus promotes a selective fertilization of eggs. The ciliation of the common duct is probably responsible for the distribution of incoming sperm among the tubules.

Bojat and Haase (2002) assessed the amount of allosperm stored in the spermatheca in relation to the structure of the spermatheca (number of spermathecal tubules) in 18 individuals of *Arianta arbustorum* that had copulated once. Snails differed in patterns of sperm storage: two individuals used 100% of their spermathecal tubules, two used 80%,

three 75%, two 66.7%, one 50%, two 40%, three 33.3%, two 25%, and one used 20%. The main tubule always contained sperm (51-100% of the total amount of sperm stored, *i.e.*, more than all lateral tubules combined). The amount of sperm stored was not correlated with the volume of the received spermatophore. However, the amount of sperm stored was positively correlated with the number of spermathecal tubules. This suggests that the female role of the receiver controls the number of sperm stored.

Baminger and Haase (1999) examined whether the variation in number of spermathecal tubules and the amount of allosperm stored are influenced by the risk of sperm competition, as indicated by the local density of adult *Arianta arbustorum* in six natural populations in the Eastern Alps, Austria. The number of spermathecal tubules ranged from two to nine. However, the six populations did not differ in either the mean number of spermathecal tubules or the cumulative length of the tubules. Individuals from different populations did not differ in the amount of sperm stored, and the amount of sperm stored was not correlated with population density. This indicates that the risk of sperm competition does not affect the number of spermathecal tubules. However, it is still not known whether individuals in high-density populations store allosperm from more different mating partners than those in low-density populations.

A histochemical analysis of the spermatheca of *Arianta arbustorum* revealed polysaccharides in the periphery of connective tissue and muscle cells (Bojat *et al.* 2003). Polysaccharides were differentially distributed in the epithelial cells of the fertilization chamber and spermatheca, indicating regions that differed in physiological activity. In general, the concentration of polysaccharides including glycogen increased towards the blind end of the spermathecal tubules. Lipids were more or less equally distributed in the epithelium along the tubules. Polysaccharides and lipids have nutritive function. The highly active epithelium could provide nutrients for the stored and active spermatozoa (Rogers and Chase 2002). However, an exchange of substances between epithelium and spermatozoa has not been observed.

BENEFITS OF MULTIPLE MATING FOR FEMALES

In many animals, males are selected to mate as many times as possible to maximize their reproductive success (Bateman 1948, Trivers 1972). For females, in contrast, the advantage of multiple mating is not so obvious. The relatively small number of ova produced by a female could be fertilized by sperm from one or very few male ejaculates, especially when the female can store sperm or has a short reproductive period. Moreover, possible costs of mating should select against unnecessary matings. While females of some species mate only once in their lives, multiple mating

by females is generally very common. Several hypotheses have been suggested to explain the adaptive significance of multiple mating by females (Birkhead and Møller 1998). Among them, the hypothesis of sperm replenishment is the most straightforward explanation for multiple mating by females. The underlying mechanism could vary: the sperm received from one male may not be enough to fertilize all the eggs produced by a female, the viability of sperm stored may decrease with time, or a mate may have transferred sperm of low quality. Another hypothesis predicts genetic advantages (multiple mating with different partners may lead to multiple paternity and thus increase the genetic variability among the offspring of a brood). Furthermore, females may enjoy nutritional benefits from repeated matings by receiving nutrients with the spermatophore. These hypotheses are not mutually exclusive.

Chen and Baur (1993) examined reproductive traits over two years in individuals of *Arianta arbustorum* that copulated several times per year (snails kept in pairs), in individuals that copulated twice (once at the beginning of each year) or once (at the beginning of the first year), and in individuals prevented from copulation (snails kept isolated). Copulations were not always reciprocally successful: 3 of 57 snails (5.3%) failed to produce fertile eggs although their mates reproduced successfully. Similarly, 2 of 15 pairs (13.3%) failed to reproduce successfully. Snails allowed to mate repeatedly within each season tended to lay more eggs than snails that mated once per year. However, the number of hatchlings did not differ significantly between the two treatment groups because eggs laid by snails allowed to mate repeatedly had a lower hatching success. Snails that remated in the second year laid more eggs with a higher hatching success, and thus produced more hatchlings, than snails that mated only once at the beginning of the first year. Snails that were prevented from mating produced a few hatchlings (by self-fertilization) in the second year; their reproductive success was less than 1% of that of mated snails. These results suggest that multiple mating is also adaptive for the female function of *A. arbustorum* by increasing female fecundity and fertility and serving as a hedge against unsuccessful copulations.

Egg production in several species of stylommatophoran gastropods is stimulated by mating behavior and/or substances derived from male ejaculate (Takeda 1983, Bride *et al.* 1991). In *Helix aspersa*, mating increases the synthesis and release of a dorsal body hormone essential for vitellogenesis, ovulation, and egg-laying (Saleuddin *et al.* 1991). Whether this activation of the dorsal body is direct, under either neural or hormonal control, or indirect under gonadal influence, is not known (Saleuddin *et al.* 1991). B. Baur and A. Baur (1992b) examined experimentally whether extended courtship display or repeated copulation in the course of a

reproductive season stimulates egg production in *Arianta arbustorum*. Clutch size decreased in successive egg batches of individuals that copulated once at the beginning of the reproductive season (a seasonal decrease in clutch size was also observed in *A. arbustorum* kept in field cages; Baur 1990a). Repeated copulation, however, was found to increase clutch size, while courtship display did not affect egg production. Repeated copulation neither accelerated the onset of egg laying nor increased the hatching success of eggs. These results suggest that reciprocal intromission and/or receipt of a spermatophore, but not the long-lasting courtship behavior, stimulates egg production in *A. arbustorum* (B. Baur and A. Baur 1992b).

MATERNAL INVESTMENT AND EGG PROVISIONING

Parental investment may often be critical to the survival and growth of young, but the larger the investment per offspring, the lower the number of offspring that can be produced. Several models have been developed to predict the optimal size of offspring under different environmental conditions. Although the models make different predictions, these are based on the assumption that egg size is a reliable measure of the amount and quality of resources invested in each offspring (*i.e.*, larger eggs are supposed to contain more organic material). A. Baur (1994) examined the within- and between-clutch variation in egg size and nutrient content of *Arianta arbustorum*. The volume of single eggs ranged from 5.5 to 26.3 mm³ (grand mean 13.4 mm³). The overall range of the nitrogen concentration of the eggs was 3.1-5.0% (grand mean 4.1%), and that of the carbon concentration 28.6-34.9% (32.2%). The nitrogen concentration indicates that eggs of *A. arbustorum* have a protein concentration of 25.5%. The within-clutch variation in egg size expressed by the coefficient of variation averaged 11.1% for egg volume and 8.3% for dry weight. Corresponding values for the concentrations of N and C were 3.7 and 1.6%. Thus, egg size was in general more variable than the nutrient concentration of the eggs. Considering mean clutch values, the nutrient contents (in mg) scaled isometrically with egg size.

Successive studies showed that not only do egg and clutch size vary seasonally but also the protein and carbon concentrations of the eggs do so (A. Baur and B. Baur 1997). Furthermore, seasonal changes in egg size and egg provisioning occur among populations (Baur and Baur 1998).

Apart from increasing egg size, maternal nutrition can be enhanced by providing hatchlings with food. Alexander (1974) suggested that if parents were unable to increase their investment in young through increasing egg size, an alternative strategy is to increase clutch size and allow some siblings to consume others (the icebox effect). The optimum

clutch size can be found by calculating the clutch size leading to maximum brood productivity, taking into account the effects of sibling cannibalism and possible trade-offs.

Maternal provision of trophic eggs of different types to hatchlings is widespread among marine gastropods. Numerous species of prosobranch snails normally produce trophic eggs, which serve as the first food for their progeny (B. Baur 1992b, 1994c). The consumption of trophic eggs can be facultative (may not occur in all egg capsules of a species) or obligate. A similar form of food provisioning has evolved in terrestrial gastropods. Hatchlings of various species of herbivorous land snails cannibalize sibling eggs (Baur 1992b). Emerging juveniles of *Arianta arbustorum* first eat their own egg shells and then the eggs of unhatched siblings, including those with fully developed embryos (Baur and Baur 1986). Egg cannibalism occurs exclusively during the hatchling stage (due to an age-specific occurrence of digestive enzymes), juvenile and adult snails being herbivorous (Baur 1987a). Cannibalistic hatchlings eat only conspecific eggs (Baur 1988c, 1988d) and do not discriminate between sib and non-sib eggs (*i.e.*, eggs from neighboring batches; Baur 1987b). Furthermore, newly hatched snails discriminate neither between fertilized and unfertilized conspecific eggs nor between eggs with well-developed embryos and eggs with less advanced embryos (Baur 1993b). Significant benefits accrue to cannibalistic hatchlings of *A. arbustorum*. Laboratory experiments demonstrated that newly hatched snails fed a cannibalistic diet during their first 10 days of life increased in wet weight 2.6 times as much as siblings fed on lettuce (Baur 1990b). In this experiment, egg consumption within 10 days ranged from 0.7 to 4.0 eggs per individual and increase in weight of cannibalistic hatchlings was positively correlated with the number of eggs consumed. Diet did not affect hatchling survival during the first 10 days, but it did influence future survival: 66.6% of the individuals initially fed on eggs attained adulthood compared to 38.0% of those fed on lettuce. Cannibalistic hatchlings tended to complete shell growth more rapidly and thus became sexually mature earlier than non-cannibalistic ones, but the two groups did not differ in adult shell size. Thus, a cannibalistic diet during the hatchling stage will give accelerated growth and higher survival.

The extent of within-batch egg cannibalism depends primarily on the hatching asynchrony of the eggs and on the hatchlings' propensity for cannibalism (Baur and Baur 1986, B. Baur 1994c). Under natural conditions, the hatching asynchrony and, as a consequence, the extent of egg cannibalism will depend also upon the type of oviposition (batches or scattered eggs), on the spatial heterogeneity of egg-laying sites, and on climatic conditions. The great variation between populations in propensity for cannibalism sug-

gests different costs and benefits of egg cannibalism in different situations (B. Baur 1994c).

SEX ALLOCATION

Reproductive resource allocation is a fundamental aspect of life history with profound ecological and evolutionary consequences. Allocation decisions in hermaphroditic plants and animals are particularly interesting because individuals can potentially maximize reproductive success through a wide variety of different strategies. Thus, a key observation for testing sex allocation theory in simultaneous hermaphrodites is the proportion of resources devoted to male vs. female function (Charnov 1982). The specific allocation strategy followed by a hermaphrodite may affect the extent of sexual selection and mating behavior (Michiels 1998). Most models of sex allocation are based on the concept of male and female gain curves (the relationship between relative investment in either male or female gamete production and resulting reproductive success; Charnov *et al.* 1976, Charnov 1982). These models have received substantial empirical support (*e.g.*, in coral reef fishes [Fisher 1981, Fischer and Petersen 1987] and in a polychaete worm [Sella 1990]). All these hermaphrodites have external fertilization. Many hermaphroditic invertebrates, however, have some form of copulation, sperm storage, and internal fertilization (Michiels 1998).

More recently, models of sex allocation for outbreeding hermaphrodites with internal fertilization and sperm storage have been developed (Charnov 1996, Greeff and Michiels 1999b). These models consider how various aspects of sperm competition, such as mating frequency, sperm digestion, and different mechanisms of sperm displacement affect sex allocation in simultaneous hermaphrodites. The models predict that a reduced mating rate leads to a reduction in resources allocated to the male function (Charnov 1996, Greeff and Michiels 1999b), while sperm digestion leads to an increase in allocation to the male function (Greeff and Michiels 1999b).

Locher and Baur (2000b) examined the effect of mating frequency on male and female reproductive output (number of sperm delivered and eggs deposited) and on the resources allocated to the male and female function (dry mass, nitrogen, and carbon contents of spermatophores and eggs) in individuals of *Arianta arbustorum*. Virgin snails were allowed to mate once, twice, or three times within a period of 51 days. Snails from the three treatment groups did not differ in shell volume. The total number of sperm delivered increased from 3,098,000 in snails that copulated once to 5,001,000 in snails that copulated twice, and to 6,849,000 in individuals with three copulations. Considering the number

of sperm delivered per copulation, however, there was no difference between snails with different numbers of copulations. Female reproductive output was not influenced by the number of copulations. Snails that copulated once, twice, or three times produced the same number of egg batches (3.9, 3.8, and 4.3, respectively) and the same number of eggs (113.7, 116.2, and 116.3) within one reproductive season. Considering snails from all treatment groups, there was a positive correlation between the total number of sperm delivered and the number of eggs produced. This indicates that individuals that delivered many sperm generally produced a large number of eggs.

In this experiment, the dry mass of spermatophores transferred averaged 0.91 mg (Locher and Baur 2000b). Spermatophores had a nitrogen concentration of 12.05%, indicating that a spermatophore on average contained 0.11 mg nitrogen. The dry mass of single eggs averaged 2.14 mg with a nitrogen concentration of 4.02%. Thus, one egg on average contained 0.086 mg nitrogen. The relative allocation to the male function (expressed as percentage of the total dry mass or amount of nitrogen devoted to the male function) increased with increasing number of copulations (dry mass: 0.58% in snails that copulated once, 0.91% in snails that copulated twice, and 1.66% in individuals that copulated three times; nitrogen: 1.72%, 2.68%, and 4.72%, respectively). However, independently of the measure chosen, reproductive allocation was highly female-biased. In none of the measures used did the average proportion of resources devoted to the male function reach 5% of the total allocation in snails that copulated three times. Considering individual snails, the maximum nitrogen allocation to the male function was 13.35% in snails that copulated three times. Thus, only a minor part of the resources available for reproduction were devoted to the male function. Furthermore, snail size did not affect the relative reproductive allocation to male or female function. The finding that an increased mating frequency leads to an increased allocation to the male function was predicted by Charnov (1996) and Greeff and Michiels (1999b), even though their models considered much higher mating frequencies (5-50 or even an infinite number of copulations). Taking into account the short period of activity of snails living in subalpine populations, the assumed range of 1-3 copulations per reproductive season might be reasonable for the animals studied.

The female skew in sex allocation found in *Arianta arbustorum* was much larger than predicted by the models of Charnov (1996) and Greeff and Michiels (1999b). A possible explanation for this pronounced female skew could be incomplete estimates of reproductive allocation to either function. In simultaneously hermaphroditic land snails like *A. arbustorum*, each mating in the male role carries costs, which include the cost of courtship behavior (e.g., the optional dart

shooting), spermatophore and sperm production, and other possible costs associated with mating. During the long-lasting courtship, gastropods produce huge amounts of mucus, an energetically expensive behavior (Davies *et al.* 1990). To my knowledge no numerical estimate of the costs of courtship behavior is available for any terrestrial gastropod. Furthermore, it is not clear whether the costs of courtship can be entirely assigned to the male function. For several reasons repeated mating might also be advantageous for the female function (see above).

A fundamental assumption of sex allocation theory in simultaneous hermaphrodites is a trade-off between male and female function, *i.e.*, the animal has a fixed amount of resources to allocate between the genders (Charnov 1982). Locher and Baur (2000a, 2000b) did not find any trade-off between the two functions. In contrast, a positive relationship between the resources allocated to the male and female functions was recorded. This result could be explained by a condition-dependent allocation and/or a "good genes" scenario. With regard to quality, any genes that affect the quality of spermatozoa and ova in the same direction would lead to a positive association between the two (Schlichting and Delesalle 1997). In hermaphroditic pulmonates such as *Arianta arbustorum*, spermatozoa and ova are produced simultaneously in the same organ, the so-called ovotestis. It would be most interesting to disentangle possible associations between the quality of spermatozoa and ova in these snails.

Trade-offs in resource allocation may not occur or may be less pronounced under favorable conditions. Under stressful conditions, such as limited food supply, high temperature, or drought, the energy intake might be carefully shared among different functions, including reproduction. Locher and Baur (2002) examined the effect of nutritional stress on mating behavior and male and female reproductive output (dry mass and nitrogen contents of spermatophores, sperm delivered, and eggs deposited) in individuals of *Arianta arbustorum* kept under three different food regimes: ample (100%), restricted (50%), and extremely restricted (25%) food supply. Independent of the extent of nutritional stress, 10-12% of the resources taken up were invested in reproductive output (both gender functions together) and 88-90% in maintenance (including feces and excretion). Courtship and copulation behavior was affected by nutritional stress. Except for one pair, snails with an extremely restricted food supply did not mate. Individuals with restricted food supply tended to court longer and copulated for a shorter period than individuals with ample food supply. Nutritional stress did not affect the number of sperm delivered. However, snails with a restricted food supply produced fewer eggs. Thus, snails kept under nutritional stress invested relatively more resources in the male function than in the female function. Nevertheless, the absolute reproduc-

tive output remained highly female biased (>95% in all experimental groups).

In hermaphroditic snails a reduced supply of protein and calcium might affect growth and alter the allocation to either sexual function. Wacker and Baur (2004) tested this hypothesis by maintaining subadult *Arianta arbustorum* on artificial diets composed of single compounds (particular amino acids, carbohydrates, fatty acids, minerals, vitamins) on an agar-based diet. Snails fed a high protein diet grew faster and reached adulthood earlier than individuals fed a low protein diet. Different calcium contents did not affect shell growth, but increased mortality when the calcium content of the food was low. Furthermore, diet-related differences in mating propensity were found.

CONCLUDING REMARKS

Much recent research effort has been directed at explaining sex-specific differences in reproductive strategies and sexual selection in gonochoristic animals. Simultaneous hermaphroditism imposes evolutionary constraints on reproducing individuals that are different from those in gonochoristic species. Yet, simultaneous hermaphrodites, in particular pulmonate gastropods, have received little attention with respect to mating strategies and sexual selection. This review summarizes the present knowledge of several aspects of sexual selection in *Arianta arbustorum*. Several other gastropod species may be well-suited for further studies on mating strategies and sexual selection. There are many topics that remain largely unexplored and there is much to be learned in this most interesting animal group.

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